Ann Microbiol (2010) 60:573–578
DOI 10.1007/s13213-010-0094-4

REVIEW ARTICLE

Biogenic amine in wines

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Received: 1 March 2010 / Accepted: 23 June 2010 / Published online: 14 July 2010

Abstract Biogenic amines (BA) are a group of organic nitrogenous compounds formed and degraded by the metabolism of living organisms (microorganisms, plants and animals). The main BA associated with wine are putrescine, histamine, tyramine and cadaverine, followed by phenylethylamine, spermidine, spermine, agmatine and tryptamine. The variability in the BA content of wine could be explained on the basis of differences in the winemaking process, time and storage conditions, raw material quality, and possible microbial contamination during winery operations. BA are formed by decarboxylation of the corresponding amino acids by microorganisms through substrate-specific decarboxylase enzymes. This property is usually strain dependent. Decarboxylase enzymes are generally induced at acidic pH and therefore they have a possible role in maintaining pH homeostasis or extending the microbial growth period by detoxification of the extracellular medium. The presence of these compounds is considered by some authors a fundamental parameter for the detriment of wine.

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Keywords Biogenic amine · Lactic acid bacteria · Risk assessment

Introduction

Biogenic amines (BA)—low molecular weight organic bases—can be formed in fermented food and beverages by bacterial metabolism via the activity of specific amino acid decarboxylases or as a spontaneous chemical reaction. The presence of BA in foods has traditionally been used as an indicator of undesired microbial activity. Relatively high levels of certain BA have also been reported to correlate with deterioration of food products and/or their defective manufacture. Their toxicity has led to general agreement that they should not be allowed to accumulate in food. BA production in foods requires the availability of precursors (i.e. amino acids), the presence of microorganisms with amino acid decarboxylases, and favourable conditions for their growth and decarboxylating activity (Arena et al. 2008). The most important BA—both qualitatively and quantitatively—in foods and beverages are histamine, tyramine, putrescine, cadaverine and β-phenylethylamine, which are products of the decarboxylation of histidine, tyrosine, ornithine, lysine and β-phenylalanine, respectively (Lonvaud-Funel 2001; Fernández et al. 2006; Landete et al. 2007). Putrescine can also be produced from arginine metabolism together with agmatine. Several food fermenting lactic acid bacteria (LAB) are able to produce BA, and genes of diverse BA-producing pathways have been identified in LAB. Interestingly, the presence of genes seems to be more strain-dependent than species-specific, suggesting that horizontal gene transfer may account for their dissemination in LAB (Lucas et al. 2005; Marcobal et al. 2006a; Coton and Coton 2009). In addition, enzymes of

pathways involved in BA production can be encoded by unstable plasmids (Lucas et al. 2005; Satomi et al. 2008), and only strains harboring BA-related plasmids are able to produce BA (Lucas et al. 2005). The amount and type of BA formed is influenced strongly by the food composition, microbial flora and other parameters that allow bacterial growth during food processing and storage. Therefore, BA production by LAB may be controlled at various levels during food fermentation, including food fermentation practices and factors involved in food fermentation processes. In this article, we summarise the physiological role and toxic effects of BA in wine, the main wine microrganisms able to produce BA, and suggested methods to reduce the BA content of wine.

Biogenic amine and relative risks

In prokaryotic cells, the physiological role of BA synthesis seems to be related mainly to defence mechanisms used by bacteria to withstand acidic environments. BA production in response to acidic stress has been extensively studied in bacteria pathogens able to produce cadaverine (Rhee et al. 2002; Lee et al. 2007). Decarboxylation increases survival under acidic stress conditions via the consumption of protons and the excretion of amines and CO_2, aiding the restoration of internal pH (van de Guchte et al. 2002). BA production may also offer a way of obtaining energy: electrogenic amino acid/amine antiport can lead to generation of proton motive force (Molenaar et al. 1993). Decarboxylase activities exhibited by LAB in acidic environments encountered during wine fermentations may therefore play a role in providing an additional mechanism for energy generation as well as acid stress tolerance.

Although BA are required for many critical biological functions, the consumption of foods containing large amounts of BA can have toxic consequences. After food consumption, small quantities of BA are commonly metabolised in the human gut to physiologically less active forms via the action of amine oxidases [monoamine oxidases (MAO), and diamine oxidase (DAO)]. Histamine can also be detoxified by methylation (via the action of methyl transferases) or acetylation (Lehane and Olley 2000). However, the intake of foods with high BA loads, or inadequate detoxification (for genetic reasons or due to the inhibitory effects of some pharmaceuticals or alcohol) can lead to BA entering the systemic circulation and causing the release of adrenaline and noradrenaline, provoking gastric acid secretion, increased cardiac output, migraine, tachycardia, increased blood sugar levels, and higher blood pressure (Caston et al. 2002). Secondary amines such as putrescine and cadaverine can also react with nitrite to form carcinogenic nitrosamines (ten Brink et al. 1990), and the adherence to intestinal mucosa of some enteropathogens, such as *Escherichia coli* O157:H7, is increased in the presence of tyramine (Lyte 2004). It has been suggested that BA have been the causative agents behind a number of food poisoning episodes, the most notorious being caused by histamine and tyramine (Taylor 1983; Silla Santos 1996).

Generally, in alcoholic beverages, the toxic dose is considered to be between 8 and 20 mg l^{-1} for histamine, 25 and 40 mg l^{-1} for tyramine, while as little as 3 mg l^{-1} phenylethylamine can cause negative physiological effects (Soufleros et al. 1998). In addition to toxicological effects, BA in wine could also affect commercial import and export since some countries have established maximum limits for histamine content in wine (Martín-Álvarez et al. 2006; Smit et al. 2008).

Biogenic amine in wine

Several amines have been identified in wine and their total concentration has been reported to range from a few milligrams per litre to about 50 mg l^{-1} depending on the quality of the wine (Anli and Bayram 2009; Smit et al. 2008; Ancin-Azpilicueta et al. 2008; Landete et al. 2005). The variability of the amine content in wine can be explained on the basis of differences in the winemaking process, time and storage conditions, raw material quality, and possible microbial contamination during winery operations (Bover-Cid and Holzapfel 1999; Lonvaud-Funel 2001; Ferreira and Pinho 2006; Smit et al. 2008). Amino acids are naturally present in grapes, representing 40% of the total wine nitrogen. Some amines are already found in grapes, namely histamine and tyramine, as well as several volatile amines and polyamines (Ancin-Azpilicueta et al. 2008; Smit et al. 2008). Putrescine and cadaverine are normally associated with poor sanitary conditions of grapes (Leitão et al. 2005). BA are produced in wines by diverse LAB, but only by strains carrying specific metabolic pathways that convert precursor amino acids into BA: the histidine decarboxylase (HDC) pathway producing histamine, the tyrosine decarboxylase (TDC) pathway producing tyramine, and two independent pathways producing putrescine, i.e. the ornithine decarboxylase (ODC) and agmatine deiminase (AgDI) pathways (Arena and Manca de Nadra 2001; Lonvaud-Funel 2001; Smit et al. 2008).

In general, the main BA produced by wine LAB species are histamine, tyramine and putrescine (Lucas et al. 2003, 2008; Marcobal et al. 2005; Smit et al. 2008). Amongst the prevalent BA, putrescine has toxic effects on man and can negatively modify wine flavour (Mangani et al. 2005). Thus it can have both health and economic consequences. Generally, putrescine is the main BA usually identified in large concentration in red wines undergoing spontaneous

malolactic fermentation. For example, in a survey performed on 27 red wines produced by wine companies located in the Apulia region (southern Italy), putrescine and cadaverine were always identified (Fig. 1). Histamine was identified in some samples and usually below 2 mg l^{-1}. Tyramine was undetected in all the samples analysed. In contrast, putrescine was always identified, at concentrations ranging from 2 mg l^{-1} to almost 10 mg l^{-1}. Isoamylamine was below the detection limits while the concentration of phenethylamine and ethylamine was usually less than 0.02 mg l^{-1} or 0.9 mg l^{-1}, respectively. Therefore, putrescine and/or putrescine producers should be targetted in Apulian wines in order to avoid putrescine accumulation.

Correlation between wine microorganisms and BA content

Yeast

A large variety of indigenous yeast species can grow and perform alcoholic fermentation in wine along with commercial *Saccharomyces cerevisiae* strains. Only a few studies have been conducted on the formation of BA by yeasts, and most only compared different yeasts species and quantified only histamine (Torrea and Ancín 2002). A number of authors reported that no remarkable increase in the concentration of BA could be observed during alcoholic fermentation, with the conclusion that yeasts do not appear to be responsible for the production of most amines found in industrial commercial red wines (Marcobal et al. 2006b). Granchi et al. (2005) even reported a decrease in BA (especially putrescine) during alcoholic fermentation while yeast dominates, for both spontaneous and induced commercial vinifications.

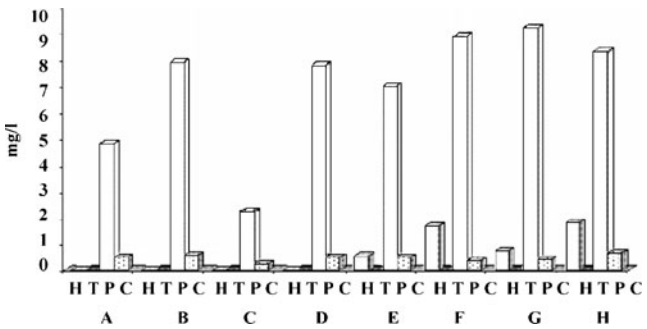

Fig. 1 Example of biogenic amines (BA) content in red wines produced in Apulian region. Red wines commercially sold (samples *A*, *B*, *C*, *D*) or collected at the end of spontaneous malolactic fermentation (samples *E*, *F*, *G*, *H*) were analysed by reverse phase HPLC (RP-HPLC). Red wines were produced by five different Apulian wineries. Graph shows mean values of three independent measurements. *H* Histamine, *T* tyramine, *P* putrescine, *C* cadaverine

Lactic acid bacteria

In contrast to the role of wine yeast on the production of BA, extensive research has been done to correlate BA production in wine with species of LAB involved in the winemaking process (Nannelli et al. 2008). BA formation in wine has long been associated mainly with non-oenococcal strains, such as spoilage *Pediococcus* and *Lactobacillus* strains, whose presence is related with high pH wine conditions (Landete et al. 2007). However, the presence of HDC and ODC pathways has been demonstrated in strains of *Oenococcus oeni*, the most suitable species to perform MLF (Marcobal et al. 2004). *O. oeni* is able to contribute significantly to the overall BA content of wines, producing mainly histamine, and the ability of *O. oeni* to produce BA varies among strains (Coton et al. 1998; Guerrini et al. 2002).

It is widely known that *Lactobacillus* and *Leuconostoc* spp. are also involved in BA production in wine. Different strains of *Lactobacillus hilgardii*, *Lactobacillus buchneri*, *Lactobacillus brevis* and *Lactobacillus mali* produce a variety of biogenic amines in wine (Moreno-Arribas and Lonvaud- Funel 1999; Moreno-Arribas et al. 2000, 2003; Martín et al. 2005; Constantini et al. 2006; Landete et al. 2007). *Lactobacillus hilgardii* X1B isolated from wine is also able to produce putrescine from arginine via two pathways. Arginine can be converted to ornithine via the arginine deiminase pathway and then ornithine is decarboxylated by the ODC to form putrescine; or arginine is first decarboxylated by an arginine decarboxylase to form agmatine, which is in turn converted into putrescine via the AgDI pathway (Arena et al. 2008). Recently a functional AgDI pathway was detected in strains of different species isolated from wine; many of these strains also contained the TDC pathway (Lucas et al. 2007). *Leuconostoc mesenteroides* has a high potential to produce tyramine or histamine in wine (Moreno-Arribas et al. 2003; Landete et al. 2007). Moreover, LAB strains have the ability to produce different amines simultaneously (Coton et al. 1998; Moreno-Arribas et al. 2000; Lonvaud-Funel 2001; Guerrini et al. 2002), suggesting that some strains might possess more than one amino acid decarboxylase activity under specific culture conditions.

LAB species able to produce BA are also strictly dependent on oenological practices and the fermentation process. Wineries may have their "own" LAB populations that can explain differences in BA contents found in regional wines. For example, although *O. oeni* is sometimes reported to be able to produce BA (Marcobal et al. 2004), *O. oeni* strains identified from different wine fermentation performed in Apulia region were unable to produce BA. Production of BA was always observed from strains belonging to *L. brevis*, *L. hilgardii* and, rarely, *L. plantarum*

species. Moreover, in addition to LAB commonly found in fermented wine, unusual wine LAB, such as *Enterococcus faecium*, were identified as tyramine producers (Beneduce et al., unpublished results).

Methods to reduce BA content in wine

Many LAB strains are used as starter cultures in several fermented foods and beverages. In general, the choice of starter cultures is fundamental in order to guarantee the quality of final products. For this reason, the inability to form BA should be an important criteria in the selection of starter cultures for the management of fermented food and beverages. Inoculation with starter cultures that are unable to produce BA is a viable option for the control of these compounds in wine (Martín-Álvarez et al. 2006).

MLF of wine generally starts spontaneously when the population of indigenous LAB reaches a sufficient level. When the conditions of wine are favourable to the development of BA-producing LAB, spontaneous MLF can lead to the accumulation of significant amounts of BA (Lonvaud-Funel 2001). In contrast, when MLF is performed under controlled conditions after inoculating the wine with a selected strain of *O. oeni* unable to form BA, the amounts of BA are markedly reduced (Divol et al. 2003; Martín-Álvarez et al. 2006). It seems that co-inoculation of *O. oeni* starter cultures together with alcoholic fermentation has the potential to control BA formation. However, the ability of malolactic starters to reduce BA contens during wine fermentation seem to be strain-dependent (Fig. 2) and non-significant differences between inoculated and spontaneous MLF are sometimes detectable. Therefore, several malolactic starter strains should be checked prior to finding a suitable starter able to reduce BA.

BA may also be oxidized by the action of amino oxidase (AO; ten Brink et al. 1990; Gardini et al. 2005). The potential role of microorganisms involved in food fermentations with AO activity has been investigated with the aim of preventing or reducing the accumulation of BA in foods. Leuschner et al. (1998) tested in vitro the potential amine degradation carried out by many species of bacteria isolated from foods and, in particular, by strains belonging to the genera *Lactobacillus*, *Pediococcus* and *Micrococcus*. Tyramine oxidase activity of several microbial strains was strictly dependent on pH, temperature and NaCl, as well as on glucose. However, amine degradation was generally restricted to aerobic microorganisms, which are of limited use in fermented foods such as wine that characteristically constitute an anaerobic environment. Recently, facultative anaerobic wine LAB strains able to degrade putrescine and tyramine were identified. The potential of these strains to control BA accumulation during wine fermentation is currently under evaluation. In addition to AO activity and the use of microbial starters unable to produce BA, agricultural and oenological practices may control BA accumulation. Indeed, viticulture region and grape varieties appear to influence the amounts of BA, since wines of some regions exhibit higher contents of amines than wines from other regions (Marques et al. 2008). The occurrence of BA in grapes could also be controlled by reducing practices that increase amino acid extraction, such as grape skin maceration and contact with the lees.

Wine fermentation parameters such as ethanol concentration and pH values may also affect the final content of BA in wine, by an indirect control of wine spoilage microorganisms such as *L. plantarum*, *L. hilgardii* and *E. faecium*. However, it should be noted that vinification techniques may also increase the BA contents in wine by increasing the availability of amino acids precursors (Ancın-Azpilicueta et al. 2010).

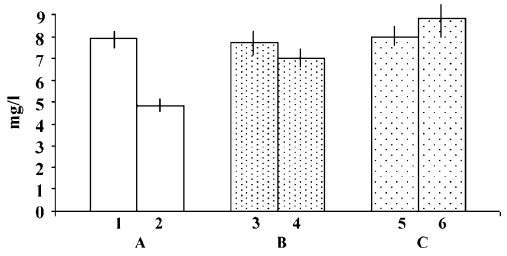

Fig. 2 Putrescine contents in Apulian red wines with spontaneous (*1*, *3* and *5*) or inoculated (*2*, *4* and *6*) malolactic fermentation (MLF). *A*, *C* MLF performed with indigenous *Oenococcus oeni*. *B* MLF performed with commercially available *Oenococcus oeni* starter. Data shown are mean±standard deviations from three independent experiments

Conclusions

Accumulation of BA in wine due to bacterial metabolism may became an health issue. However, the amount and types of BA detectable in wines are reported to have regional variability and are strictly dependent on several factors including agricultural and oenological practices. Putrescine is often the main BA detectable in wine, and a correlation between putrescine content and LAB able to decarboxylate ornithine or to metabolise arginine and agmatine is generally observed. Monitoring BA content during wine fermentation is a worthwhile goal in order to identify problems related to, for example, wine fermentation or wine spoilage microorganisms and provide solutions to avoid BA accumulation in wine. Indeed, it should be noted that BA content in wine is usually under the limits considered as a risk and we currently have the opportunity to transfer our now greatly increased scientific knowledge in order to avoid BA risks in fermented beverages.

Acknowledgement This work was funded by the EU commission in the framework of the BIAMFOOD project (Controlling Biogenic Amines in Traditional Food Fermentations in Regional Europe—project n°211441).

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